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THE RESPIRATION OF AQUATIC INSECTS.

A Collective Review.

BY RICHARD A. MUTTKOWSKI, PH.D., University of Idaho.

1. *Introductory.*

The present paper constitutes a collective review of work of the past fifteen years on the respiration of aquatic insects. Among the more important workers in this field the following may be named: Brocher, Portier (France); Böving, Blunck, Krogh, Wesenberg-Lund (Denmark); Ege (Sweden); Franckenberg (Germany); Tillyard (Australia).

When we speak of aquatic insects, we usually mean that the particular insects are aquatic in their larval stages—hence that they lead an *amphibious* life, aquatic in the larval stage, terrestrial in the adult state. An absolute division cannot be made, as insects possess varying degrees of aquaticity. The distribution of aquatic life among the orders is as follows:

Orders entirely amphibious: Odonata, Perloidea, Ephemeroidea, Trichoptera.

Orders in part amphibious:

Coleoptera: Parnidæ, Haliplidæ, Gyrinidæ, Hydrophilidæ, Dytiscidæ, Galerucinæ, etc.

Diptera: Psychodidæ, Corethridæ, Chironomidæ, Culicidæ, Stratiomyidæ, Tipulidæ, Simuliidæ, Dixiidæ, in part or wholly, etc.

Hemiptera: Corixidæ, Belostomatidæ, Naucoridæ, Notonectidæ, etc.

Hymenoptera: some parasites (some Trichogrammatidæ, etc.).

Lepidoptera: Nymphalinæ, some Noctuid genera.

Megaloptera: Sialidæ, *Corydalis*.

Neuroptera: Hemerobidæ.

It should be noted that the amphibious habit is not confined to a few orders, but that it may occur anywhere. It may be that the entire family leads an amphibious life, or that a single genus of a family is amphibious. Thus, among the Ceratopogonidæ, one section is completely terrestrial in habit, while the remainder is amphibious; among the Chrysomelidæ, the subfamily Galerucinæ is aquatic, the remainder terrestrial. Again, among aquatic Coleoptera we find nearly uniformly that the adults also are amphibious, while in all other orders the adults spend their lives above water, although a number of genera are known in which the adult enters the water for prolonged period for oviposition (*Enallagma* and *Aeschna* among Odonata, many Trichoptera, especialy micro-Trichoptera, for periods from one half to six hours).

Two terms used frequently in this paper will need definition: *surface-breathers* and *water-breathers*. By *surface-breathers* such animals are designated as come to the surface of the water to renew their oxygen,—that is, they breathe atmospheric air. *Water-breathers* are all animals that obtain their oxygen in solution directly from the water. The dividing line between these two categories cannot be as sharply drawn as one might suppose, for the degree of aquaticity is variable. For instance, as will be shown later, surface-breathers may become temporary water-breathers.

Among water-breathers two types of breathing exist: an *internal oxygenation, i.e.*, the oxygen exchange takes place within the body (*e.g.*, Odonata larvæ, Chironomid larvæ) ; and *external oxygenation, i.e.*, the oxygen exchange takes place outside of the body (*e.g.*, adult beetles).

2. *General Physiology of Respiration.*

The principle involved is that of a diffusion of gases through a moist membrane. We all know that obeying the laws of gas diffusion gases will tend to form an equilibrium on both sides of a moist membrane; or, if in solution, on both sides of a membrane separating two liquids. Such is, simply put, the condition in an aquatic insect. There is a certain gas pressure in the body of the insect; the water around the insect contains gas in solution; a membrane, the cuticle plus hypodermis, separates the two, and throughout the membrane the gases tend to equilibrate.

In aërial respiration of insects the dry atmospheric air is led by the tracheæ and tracheoles directly to the cells where it passes into solution in the cell cytoplasm. The process is assisted by inspiratory movements of abdomen and thorax and by the closing mechanism of the spiracles. Fundamentally, however, the principle of respiration in aquatic insects is that of a gas balance of two sides of a membrane. This has been definitely called a *diffusion* theory in contradistinction to the older *secretion* theory.

3. *Internal Oxygenation.*

By internal oxygenation is meant that the oxygen renewal takes place within the body, or at least at the surface of a membrane, —much as in our own lungs, or as in the gills of fish. There are two methods found in insects. Briefly, these may be called the *tracheal*, or *gaseous* method, and the *fixation*, or *solution* method. In the *tracheal* method the oxygen goes out of solution at once and is carried to the tissues in gaseous form by the tracheoles. In the *fixation* process the oxygen passes through a membrane and is fixed by a respiratory pigment in the blood plasma, and passes out of solution later on.

The tracheal method has been studied very extensively among insects, and primarily in the Odonata. In several excellent papers Tillyard has taken up the Odonate respiration in a very thorough manner, particularly that of the lantern type of rectal gills found in dragonfly larvæ (suborder Anisoptera). Damselfly larvæ, of the suborder Zygoptera, breathe by means of caudal leaf-like gills.

In gross structure, the morphology of the rectal gills has been likened to a Japanese lantern, that is, the gill lamellæ are arranged in six rows. These six rows are possessed by all Anisopteran larvæ, but modified in several ways. Thus there may be six rows of simple lamellæ, or six rows of double lamellæ. There is another classification into undulate, implicable, foliate and other types of gill lamellæ, depending on the species. For further details I must refer to the papers of Tillyard listed in the bibliography.

Histologically, the structure of one of the gill lamellæ is as follows: The lamellæ are supplied with tracheal trunks, from which short branches supplied with many tracheolar loops extend into the lamellæ, *i.e.*, afferent and efferent capillaries, similar to the blood capillaries of the gills in fish. In cross section each plate is seen to be a lamella, each side one layer in thickness, with a very thin outer cuticle. The cell layer is a modification of the rectal epithelium and forms a syncitium in which the tracheoles are imbedded. The tracheal capillaries lead back to the collecting tracheæ, these to the tracheal trunks which carry the oxygen to all parts of the body, there to be taken up by the smaller vessels and to the tissue cells. The number of tracheolar loops in such a rectal gill has been estimated as varying from 10,000 to 90,000, according to the type of gill possessed by the respective species.

As the gas is used up in the tracheæ there is a diffusion from the region of higher partial pressure outside (in the water) to the region of lower partial pressure within, the gas going out of solution at once in the lumina of the tracheoles. The motion of the rectal gills is to supply a fresh current of water. The composition of the air in the tracheæ is the same as in the water, that is, in the proportions of 65 parts nitrogen to 35 oxygen, as compared to the atmospheric 80 parts nitrogen to 20 oxygen. (This is at zero temperature. The amount of oxygen in solution varies with the temperature of the water, being greatest at zero.) The latter composition has been determined with an apparatus devised by Krogh which is able to measure extremely minute quantities of the gases.

Since very little nitrogen is used up there is a constant nitrogen equilibrium, while a continuous flow of oxygen takes place. The same is true for carbon dioxide, since there is already an overbalance in the blood in the form of carbonic acid.

The topic of gases entering in solution raises the question: how do gases leave aquatic larvæ? (See section 9 for expiration of adults.) In aquatic insects there is only an afferent stream of gas through the tracheæ to the tissues. Oxygen flows to the cells and is used up in oxidation, and carbon dioxide is formed. What becomes of the carbon dioxide? We know that it is taken up by the blood. But how does it leave the body? The hypothesis was suggested by Tillyard that it probably would go out through thin places in the epidermis in the form of carbonic acid. Personally I was able to show that this hypothesis might apply. In some experiments on the permeability of chitin membranes I was able to show that not only thin portions, but also thick portions of a chitin membrane will very readily permit the passage of carbonic acid in practically all parts of the body. What I did not show was that this passage actually takes place in the living insect. But if a stripped chitin membrane shows such a considerable degree of permeability to the flow of carbonic acid, it can be assumed that it may show a similar degree of permeability in the living aquatic insect. It would then once more be a question of simple diffusion.

In the Zygoptera we meet with a somewhat different type of structure. There are three caudal gill plates, each supplied with tracheal trunks, the middle one with four, the lateral one with two each. As the tracheæ are often pigmented and as their type of branching is distinctive of the species they are used as taxonomic characters. Histologically, a cross section shows the outer cuticle, hypodermis, the two or four tracheal trunks lying in a network of alveoli, and a dorsal and ventral blood channel. The alveoli appear to be derived from the hypodermis, and form ingrowths filling the gills with a meshwork. Their function is obscure. The tracheal trunks break up into smaller trunks, and these into tracheoles, which then form an anastomosing network, not simple and numerous loops in lamellar form as in the Anisoptera, but a fairly elaborate series of anastomosing loops.

The difference between Anisoptera and Zygoptera is then that in the latter the oxygen must pass through a thick outer cuticle, the cellular hypodermis beneath, then to be taken up the tracheal capillaries which lie in the alveolar meshwork. It will be seen at once that the Anisopteran system is highly specialized compared to that of the Zygoptera. In the Zygoptera, however, the capillarization of the caudal gills appears to be not the only source of oxygenation. In experimenting on the necessity of the caudal gills to the life of damselfly larvæ I removed the caudal gills (there is a special breaking point at the base of each gill) in successive instars; while there was regeneration following each amputation, this took place only during ecdysis, and the newly formed gills were at once removed. The presence of a breaking joint in itself indicates that the organism can exist without the caudal gills, while the very copious sternal capillarization of the abdominal segments may be quite efficient in supplying the respiratory wants of the animal in the absence of the gills.

Among insects the respiration of Anisopteran Odonata is unique; and while the principles derived from its study apply generally, yet the strutcures of other insects are rather more like those of Zygoptera. Thus, may-flies and stone-flies have both lateral and caudal gills with a tracheal capillarization much like that of the Zygoptera. There is also the point that in aquatic insects so much of the structure cannot be understood unless one enters into a discussion of the phylogeny. For this there is no place in this paper. Yet the following may be noted: We have what we may call primarily amphibious groups such as stone-flies, may-flies and Odonata, and secondarily amphibious groups which include other aquatic forms. That is, the first have retained their original amphibious habits as indicated by fossils back to carboniferous times, while the others became terrestrial and then secondarily aquatic. Among the latter are to be included the Trichoptera, Coleoptera, Diptera, and Hemiptera.

Fixation Method.—Another method of internal oxygenation is that of fixation of oxygen by some carrier in the blood. In a few rare cases the carrier is colored. Thus, in some species of

Chironomidæ, the pigment is hemoglobin, like that of vertebrates, except that it is found in the plasma, and not within the corpuscles. The morphology of the blood gills is extremely simple. The gills consist of sacs everted from the body. They have a very thin cuticle, and a hypodermis, and their lumen is continuous with the hæmocoel, so that blood can freely flow into the sacs and out again. The oxygen diffuses through the epidermis just as in the case of vertebrates and is fixed by the hemoglobin or other carrier (perhaps hemocyanin?) in the blood. Just what this other carrier may be is not definitely ascertained. But by far the larger number of aquatic insects have no visible colored carrier or respiratory pigment. Thus, for example, Trichoptera larvæ, the larvæ of *Simulium,* of Culicidæ, and of most Chironomidæ, have gill pouches, usually placed at the caudal end, but all without any visible indication of a respiratory pigment. There is need of more work on this phase of the subject.

4. *Transportation of Air to the Tissues.*

The question of how air is taken up by the cells is still in doubt. Portier claims that the tracheoles end blindly in the individual cells, according to observations made with polarized light. Then there is the older claim that they end blindly at the cell walls, and there is the newer supposition that the tracheoles form capillary loops similar to those at which oxygen enters in the gill lamellæ and also similar to the capillaries of the vertebrates, and that the oxygen passes very readily out through the capillary wall and cell membrane wherever needed. All three theories remain to be proven. But the general cycle of air absorption and transportation can be outlined readily. There are several types of cycles.

a. Atmospheric air—enters tracheæ and tracheoles—passes into solution in cell cytoplasm (all terrestrial insects, all surface-breathers).

b. Atmospheric air—passes into solution in water—passes through membrane and tracheal wall—goes out of solution in lumina of tracheæ—passes into solution in cell cytoplasm. Hence twice in gaseous form and twice in solution till used. (All water-breathing hemimetabola, all Trichoptera larvæ and pupæ, all water-breathing beetle larvæ, all water-breathing Chironomidæ, Corethridæ, and Psychodidæ, etc.)

c. Atmospheric air—goes into solution in water—passes through membrane—is fixed by blood—passes through tracheal walls—out of solution in lumina of tracheæ—into solution in cell cytoplasm. (All holaquatic Diptera, and probably Trichoptera.)

d. Atmospheric air—goes into solution in water—passes through body wall—is fixed by blood—carried by blood to tissues—out of solution in cell cytoplasm. (? Some Chironomidæ larvæ. Hydrachnida ?.)

We have here a progressive order of complexity, wherein the tracheal method tends to persist, but is finally dropped. Many Chironomidæ that have the fixation method well developed also show an elaborate tracheation. Others again show mere vestiges of tracheæ. In the latter it seems rather probable that the respiration is similar to that of other non-tracheate Arthropoda, *i.e.*, the tissues are bathed directly by the blood and the tissues extract their oxygen supply from the blood as they need it. Still more confusing is the fact that in so many Chironomidæ without tracheæ, or only with vestigies, there is no visible carrier.

As an appendix to this section I would note certain filamentous structures which do not contain tracheæ, but which seem to act as respiratory organs and which connect up with tracheæ. Such are the gill filaments in the larvæ of the water-penny *Psephenus*, in caddisworms, the dorsal tufts in the pupæ of *Simulium* and Psychodidæ.

(*Continued in December* Bulletin.)

DISTRIBUTIONAL NOTE ON TWO SPECIES OF COLEOPTERA.

By H. M. Parshley, Smith College, Northampton, Mass.

In view of the forthcoming Catalogue of North American Coleoptera in preparation by Leng, I would place on record the following data.